Patterns of variation in cranial size and shape in two coexisting gerbilline rodents

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Abstract

Patterns of cranial variation within and between two coexisting gerbilline rodents from the Namib Desert were assessed. Size of individual cranial characters is more variable in *Desmodillus auricularis* than in *Gerbillurus paeba*, but *G. paeba* is more variable in aspects of morphological shape. This contrasting pattern of variability in size and in shape has implications for ecomorphological studies. Without information on the relative functional importance of these two aspects of morphology, there appears to be little basis for using data on morphological variation to derive ecological generalizations. It is suggested that the strikingly different degree of correlation among cranial measurements in these two species is related to differences in growth rates and demographic seasonality.

Introduction

A variety of hypotheses have suggested relationships between intrapopulation morphological variability and ecological patterns. One of the most popular and widely-tested is the "niche variation" hypothesis (Van Valen 1965 a) which argues that populations occupying wider niches should be morphologically more variable than those with narrower niches (see also Hamilton and Johnston 1978; Patterson 1981, 1983; Rothstein 1973; Soule and Stewart 1970; Van Valen and Grant 1970; Willson 1969; Willson et al. 1975). Other examples of hypotheses relating morphological variation and particular aspects of ecology were summarized in Hespenheide (1973), Weins and Rothenberry (1980), Werner and Gilliam (1984) and Futuyma and Moreno (1988). Tests of these hypotheses have yielded varying outcomes and a number of authors (Patterson 1881, 1983; Rothstein 1973; Soule and Stewart 1970, Weins and Rotenberry 1980; Willson et al. 1975) have discussed problems with the formulation of these hypotheses or the way they commonly have been tested. Recently, Schmitt et al. (1995) suggested the "niche-width" (= niche variation) hypothesis to explain the association of genetic and ecological variability in fruit bats in the Indonesian Archipelago. However, their results indicated no correlation with morphological variability.

A basic premise of these ideas is that morphologically different individuals within a population differ in patterns of resource use. The degree of difference among individuals (i. e., variation) should thus parallel the variety of a population's ecological patterns (e. g., geographical range, range of prey sizes, or some more general measures of niche breadth). The expectation that morphological variation should translate into functional variation is entirely reasonable. However, most tests of these hypotheses have rested on the additional assumption that functional variation is most importantly influenced by variation in size (sensu stricto) of morphological structures. Constraints of body size and size of particular structures, of course, are of unquestionable functional importance. Several

authors have demonstrated that differential resource use (either between species or among individuals of a single species) may be related to variation in linear dimensions of anatomical traits (most frequently examined have been trophic structures; Abbott et al. 1975, Grant 1981; Herrera 1978; Pulliam and Enders 1971; Willson 1971). In other cases, however, relationships between variation in size and variation in function have been assumed but not directly tested (see Patterson 1983 for a review). The shortcoming of this approach is illustrated by the existence of structures in which size per se may not be of clearly greater functional importance than aspects of morphology like shape or relative proportions of component parts (for mammals see Brownfield and Wunder 1976; Herring and Herring 1974; Nelson and Shump 1978; Freeman 1979; Thorington and Heaney 1981; and, Smith 1993; Russel and Thomason 1993 for reviews).

In this study we present data on contrasting patterns of variation in size and shape or proportion of cranial characters in two coexisting gerbilline rodents from the Namib Desert of Namibia. The results demonstrate the virtual necessity of understanding the relative functional importance of size/shape variation in eco-morphological studies.

Additionally, we discuss possible developmental and demographic correlates of morphological differences between these two species.

Material and methods

Specimens Examined

The two species of gerbilline rodents considered were *Gerbillurus paeba* (Smith 1836) and *Desmodillus auricularis* (Smith 1834). Specimens used in assessing morphological variability were collected at *Gorrasis* (25°18′ S, 15°55′ E) on the eastern edge of the Namib Desert in Namibia. Specimens were collected in a single habitat (the bush plain habitat of Christian 1979 a, 1980) more or less evenly throughout the period between March 1974 and April 1975. Our sample is, thus, temporally and spatially very consistent. Cranial sutures were well ossified in all specimens and there was at least slight wear on the molar teeth. Additionally, body weights of all specimens were well above minimum weights of reproductively active animals observed in the field. Therefore we feel that these specimens were both morphological and potentially reproductive adults. Precipitation essentially failed completed on the study site a year prior to the start of the field work during which the animals were collected. Rodent populations consisted of only widely scattered individuals when field work began in 1974 (Christian 1979 a, 1980). Thus, the sample consisted almost entirely of animals born during 1974–1975.

Morphological Characters

Several of the morphological characters we selected almost certainly have a direct relationship to feeding (incisor width, length of maxillary and mandibular toothrows; Smith 1993) and predator detection (length and width of auditory bulla; Lay 1972). While the functional significance of the other characters chosen (skull length, zygomatic breadth, and diastemal length) is less clear, these structures are likely related to feeding (sensu lato; see Smith 1993 for a review of morphological studies of the mammalian feeding apparatus).

The eight cranial characters were measured with dial calipers to the nearest 0.1 mm. To insure accuracy of the measurements, each specimen was measured at least twice, one week apart. If the second measurement deviated by 0.1 mm or more, it was measured a third time. In our second series, less than 10 per cent of the original measurements had to be repeated.

Analyses

The mean body weight of specimens was 24 g in *G. paeba* and 45 g in *D. auricularis*. Because of this size difference, we log-transformed the raw data before computing variances (Lewontin 1966; for rationale, see Moriarity 1977). The log-transformations scale the raw data so that variances of measurements of different magnitude are comparable while preserving the relative variability. Using log-transformed data we computed variances for each character in each species/sex class. These variances

were compared between sexes within each species and within sexes between species by a series of F-tests.

One technique used to examine questions about variation in shape or proportion was to compute Pearson product-moment correlation coefficients (r) between each pair of characters within each sex and species. We assume that a high degree of correlation among cranial characters is indicative of relatively low variation among individuals in cranial shape. Differences between species and sexes in the distribution of significant F-tests and correlation coefficients were tested for independence by Chi-square.

Another method to examine relationships among cranial characters was to compute the proportion of variation unique to each character. This was accomplished by performing a Principal Factor Analysis (PFA) in which we forced the procedure to extract eight new multivariate factors (NIE, et al. 1975). The procedure calculated an estimate of the communality (h^2) for each character. The communality expresses the proportion of the total variance of each character that is due to intercorrelations with the other characters. From this value, we calculated a uniqueness index ($1-h^2$) for each character (i. e., the proportion of the total variance of that character that cannot be attributed to correlations with the other characters).

Results

The distribution of measurements for both species gave no indication of bi- or poly-modality, indicating that the size variation discussed here is continuous. Univariate comparisons showed no significant difference in variability between sexes within each species. Univariate comparisons by sex between species indicated that all variances were larger in *D. auricularis* than in *G. paeba* (Tab. 1). F-tests on these variances indicated that *D. auricularis* was significantly more variable than *G. paeba* in six of the eight characters for females and in seven of the eight characters for males. A Chi-square test of independence on the distribution of significant F-test results was significant for either probability of the F-tests ($X^2 \geq 4.00$, $P < 0.05$, df = 1). These results indicate that the number of significantly larger variances in *D. auricularis* was greater than would be expected due to chance alone. Thus, in terms of size of cranial characters, *D. auricularis* is clearly more variable than *G. paeba*.

Table 1. Variances of log-transformed measurements of cranial characters in male and female *Desmodillus auricularis* and *Gerbillurus paeba*. Probability (P) based on F computed as S^2 for *D. auricularis* divided by S^2 for *G. paeba*.

	Males					Females				
	D. auricularius		*G. paeba*			*D. auricularius*		*G. paeba*		
CHARACTER	N	S^2	N	S^2	P	N	S^2	N	S^2	P
Skull Length (SL)	17	0.002504	28	0.000738	<0.005	18	0.002319	25	0.000559	<0.001
Zygomatic Breadth (ZB)	17	0.001941	28	0.001107	<0.100	18	0.001834	22	0.000715	<0.025
Incisor Width (IW)	18	0.005859	30	0.002473	<0.025	19	0.004438	25	0.002998	<0.25–0.10
Diastemal Length (DL)	18	0.003680	30	0.002057	<0.100	19	0.003092	26	0.001239	<0.025
Maxillary Toothrow (MT)	18	0.002590	30	0.000890	<0.010	19	0.001522	26	0.000782	<0.100
Auditory Bulla Length (BL)	18	0.001981	30	0.001015	<0.100	19	0.002448	26	0.000573	<0.100
Auditory Bulla Width (BW)	18	0.001190	30	0.001038	<0.500	19	0.001142	26	0.000700	<0.25–0.10
Mandibular Toothrow (MdT)	18	0.002010	30	0.000576	<0.005	19	0.002228	26	0.000741	<0.010

Correlation coefficients (r) for each pair of characters for each species and sex are shown in table 2. The discrepancy between sample sizes in tables 1 and 2 result from the fact that correlation coefficients were computed using data from specimens for which all eight cranial measurements were available. The number of significant r's is distributed as follows: in females, *D. auricularis* had 20 of the possible 28 r's significant at P < 0.05, with two additional r's significant at 0.05 < P < 0.10, while *G. paeba* had only 9 r's significant at P < 0.05 and 1 further r significant at 0.05 < P < 0.10. In males, *D. auricularis* had 27 of the 28 r's significant at P < 0.05 and the other r significant at 0.05 < P < 0.10; *G. paeba* had only 16 r's significant (all at P < 0.05). Sample sizes were larger in *G. paeba* than in *D. auricularis* for both sexes. Our statements about differences in the degree of correlation in cranial characters in these two species are therefore conservative.

Table 2. Character correlation matrices for male and female *Desmodillus auricularis* and *Gerbillurus paeba*. Abbreviations follow table 1. Significance levels of correlation coefficients (r), * = P < 0.05; ** = 0.05 < P < 0.10.

		D. auricularis females (n = 17)							D. auricularis males (n = 15)					
	ZB	IW	DL	MT	BL	BW	MdT	ZB	IW	DL	MT	BL	BW	MdT
SL	.760*	.569*	.965*	.614*	.889*	.616*	.250	.875*	.589*	.887*	.772*	.910*	.747*	.651*
ZB		.575*	.761*	.547*	.850*	.657*	.441**		.510**	.859*	.759*	.883*	.626*	.678*
IW			.617*	.394	.505*	.096	.108			.680*	.674*	.516*	.652*	.714*
DL				.451**	.839*	.508*	.135				.747*	.791*	.702*	.596*
MT					.674*	.585*	.724*					.760*	.618*	.887*
BL						.750*	.373						.766*	.643*
BW							.495*							.537*

		G. paeba females (n = 18)							G. paeba males (n = 26)					
	ZB	IW	DL	MT	BL	BW	MdT	ZB	IW	DL	MT	BL	BW	MdT
SL	.646*	.230	.853*	.339	.737*	.576*	.277	.817*	.239*	.896*	.425*	.728*	.692*	.166
ZB		.107	.589*	.345	.556*	.608*	−0.17		.210	.781*	.427*	.695*	.712*	.263
IW			.078	−.017	−.013	−.122	.216			.207	.436*	.211*	.144*	.547*
DL				.243	.613*	.436**	.081				.258	.686	.722*	.098
MT					.308	.387	.328					.391*	.253	.486*
BL						.660*	−.005						.686*	.256
BW							.159							.163

The distribution of significant r's was also tested for independence by Chi-square. Between sexes within species, there were no significant differences in the number of correlated characters ($X^2 = \le 1.0$, P > 0.3). The number of significant correlations was greater in female *D. auricularis* than in *G. paeba* ($X^2 \ge 4.1$, P < 0.05 for either level of significance of r, df = 1). In males, there were more significant r's in *D. auricularis* than in *G. paeba* ($X^2 = 3.27$, 0.05 < P < 0.10, df = 1).

The proportion of the total variance unique to each character ($1-h^2$) is presented in table 3. The uniqueness values for *D. auricularis* were low (averaging 0.12 for males and 0.10 for females) compared with the mean values in *G. paeba* (0.23 and 0.34 for males and females, respectively). In all but 3 of 16 cases (two in males and one in females), uniqueness values for cranial measurements of *G. paeba* were greater than for those of *D. auricularis*. These values, and the correlation analyses described above, indicate that dimensions of cranial characters in *D. auricularis* are highly intercorrelated. These same

characters in *G. paeba* are relatively independent of each other. Thus, as indicated above, the size of individual cranial characters is more variable in *D. auricularis*, but the interrelations among cranial characters (i.e., relative proportions or shape) are considerably more variable in *G. paeba*.

Table 3. Proportion of variation that is unique $(1-h^2)$ for each cranial character in *Desmodillus auricularis* and *Gerbillurus paeba* using the full factor analysis model (NIE et al. 1975). See text for further explanation.

	D. auricularis		G. paeba	
	Males	**Females**	**Males**	**Females**
SL	0.073	0.000	0.050	0.000
ZB	0.048	0.048	0.109	0.303
IW	0.039	0.265	0.406	0.649
DL	0.008	0.016	0.034	0.166
MT	0.079	0.042	0.377	0.597
BL	0.574	0.026	0.268	0.239
BW	0.126	0.162	0.252	0.263
MdT	0.032	0.207	0.368	0.465
Mean	0.122	0.096	0.233	0.335

Discussion

Our initial intent in this study of morphological variation was to test the niche variation hypothesis. Field data suggested that *D. auricularis* occupies a broader niche than *G. paeba*. Accordingly, we predicted that the former species would be morphologically more variable, in the classical size dimension, than the latter. Part of this prediction was based on differences between these two species in demographic seasonality: reproduction, recruitment, and population growth in *G. paeba* are highly seasonal, whereas the demographic pattern of *D. auricularis* is less seasonally restricted (CHRISTIAN 1979 a, 1980). There appears to be a direct relationship in desert rodents between reproduction/population growth and availability and use of resources (BEATLEY 1969; CHRISTIAN 1979 a; FRENCH et al. 1974; REICHMAN and VAN DE GRAAFF 1975; PERRIN 1986). We assume that an organism's use of time or of temporally variable resources is an important aspect of the niche. Therefore, we view the demographic aseasonality of *D. auricularis* as indicative of a relatively broad temporal niche. Additionally, although both species occur in a variety of habitat types (ranging from sand dunes to boulder strewn plains), *D. auricularis* is more consistently present in a range of habitats than is *G. paeba* (CHRISTIAN 1980), further suggesting a broader niche for *D. auricularis*.

   Our morphological results indicate that *D. auricularis* is more variable than *G. paeba* in size of cranial characters but less variable in cranial shape (correlation among characters). Some workers (OLSON and MILLER 1958; FRAZETTA 1975; SMITH 1993; ATCHLEY 1993; RUSSELL and THOMASON 1993; EMERSON and BRAMBLE 1993) have suggested that highly correlated characters may operate as an integrated functional unit. Thus, differences in functional variability of the skulls of these two species may relate not only to differential size but also to differences in the constancy of relations among component parts. Patterns of variation like the ones observed in this study have clear implications for the niche variation model and for other eco-morphological hypotheses. That is, if differences between these species in niche breadth are related to size variability, the observed trends are consistent with predictions of the niche variation hypothesis. However,

if functional variability and niche breadth in these species are closely associated with variation in cranial proportions (correlations), the morphological data are contrary to the predictions. As in most similar studies, data on specific functions of cranial structures of these two rodent species are unavailable. Therefore, in this and similar cases, we believe that there is little basis for deriving ecological generalizations from data on morphological variation.

The different degree of correlation among cranial measurements in these two species is rather surprising, and it is of interest to consider possible sources of this difference. Several authors (Bock and von Wahlert 1965; Olson and Miller 1958; Van Valen 1965 b; Atchley 1993) have stressed the general importance of developmental processes in influencing correlations among morphological characters. Published growth data for G. paeba, are, to our knowledge, unavailable. In D. auricularis, body length, hind foot length, and weight increase relatively steadily from birth to 45 days of age (Nel and Stutterheim 1973). Attainment of adult mass in this species is quite slow (Birkenstock and Nel 1977). In plotting log body weight versus log skull length or log maxillary toothrow length for both juveniles (not included in samples used in the above analyses) and adults, we find strikingly different patterns in these two species. In both male and female D. auricularis, these plots increase relatively linearly. In contrast, in G. paeba there is an asymptote with an inflection point at body weights of 18–29 g. Linear regression of log skull length against log body weight explains a higher proportion of the variation in skull length in D. auricularis (coefficient of determination, r^2, 0.68 to 0.81) than in G. paeba (r^2 of 0.40 to 0.56). These same patterns hold even among the morphologically defined adults used in the above analysis of variability. While we lack absolute time scales for growth data, it appears that G. paeba reaches full growth more rapidly than does D. auricularis, or at least completes growth at lower body weights relative to maximum weight. It is likely that the differences in cranial correlation in these species are related to the different rates and patterns of growth.

Gould (1977) suggested a trade-off between "perfection and morphology" and production of offspring. We presume that a high degree of correlation among morphological characters may be viewed as one aspect of morphological "perfection", and suggest, in a manner at least superficially similar to Gould's argument, that differences in cranial correlation in these species are related to life history differences. The desert environment where field studies were conducted is strongly seasonal and, as described earlier, the two species differ in the degree to which their demographic patterns are tied to seasonal events. In addition to G. paeba's highly seasonal pattern of reproduction, recruitment, and rapid population growth, this species differs from D. auricularis in other ways associated with demographic seasonality (Christian 1979 a, b, 1980). Gerbillurus paeba produces larger litters, has somewhat shorter life expectancy, and, as noted above, is of smaller body size and appears to reach morphological adulthood at relatively lower body weights.

G. paeba reproduces primarily during times of high water availability. The provision of drinking water in the field extended the length of the breeding season up to several months in this species (Christian 1979 a). Christian (1979 b) found that G. paeba is physiologically less capable of conserving water than is D. auricularis. He argued that, because of its higher water needs, G. paeba is limited to carrying out important reproductive functions (which may entail considerable water demands) over a more restricted portion of the year. Thus, relatively high seasonality may be obligatory in this species (see also Ascaray et al. 1991). In such a species, natural selection may be expected to favor the rapid development of particular characters that are critical for capitalizing on resources necessary for successful reproduction, perhaps at the expense of the development of other, less immediately important characters. This growth may lead to the relatively poorly "integrated" cranial morphology observed in G. paeba. In

D. auricularis, on the other hand, where there is apparently not a premium on extremely rapid demographic response, natural selection may favor a somewhat different developmental pattern and allow the production of a highly conservative cranial morphology compared to *G. paeba*. In a species with the demographic characteristics of *G. paeba*, natural selection likely favors individuals devoting a relatively high proportion of available resources to reproduction. Conversely, natural selection in a more aseasonal species, such as *D. auricularis*, may favor individuals that devote a relatively greater proportion of the available resources to non-reproductive functions (growth and maintenance). The differential allocation of materials to either reproductive functions or to other activities would explain the differences in cranial morphology between these two demographically different, coexisting species.

Zusammenfassung

Variationsmuster von Schädelgröße und Schädelform bei zwei syntopen Nagetier-Arten (Gerbillinae, Rodentia)

Bei *Gerbillurus paeba* und der rund doppelt so schweren Art *Desmodillus auricularis* aus der Wüste Namib (Namibia) wurde anhand von 8 linearen Schädelmassen die inner- und zwischenartliche Variation untersucht. Dabei zeigte sich das folgende Bild: *D. auricularis* weist die höhere Variabilität in der Schädelgröße auf, *G. paeba* eine höhere Variabilität in der Schädelform. Dieser scheinbar widersprüchliche Befund bei Bewohnern eines identischen Lebensraumes wirft öko-morphologische Fragen in bezug auf die Interpretation der „Nischen-Variations"-Hypothese auf. Vermutlich besteht ein Zusammenhang mit der unterschiedlichen Populationsentwicklung zwischen den beiden Arten: *G. paeba* weist eine deutlich höhere Saisonalität in Fortpflanzung und Populationswachstum auf: *D. auricularis* nutzt dank ihrer geringeren Saisonalität eine größere zeitliche Nische.

Literature

Abbott, I.; Abott, L. K., Grant, P. R. (1975): Seed selection and handling ability of four species of Darwin's Finches. Condor **77**, 332–335.

Ascaray, C. M.; Perrin, M. R.; McLachlan, A.; Els, S. F. (1991): Population ecology of the hairy-footed gerbil, *Gerbillurs paeba*, in a coastal dunefield of South Africa. Z. Säugetierkunde **56**, 296–305.

Atchley, W. R. (1993): Genetic and developmental aspects of variability in the mammalian mandible. In: The Skull, Vol. 1. Ed. by J. Hanken and B. K. Hall. Chicago, Illinois: Univ. Chicago Press. Pp. 207–247.

Beatley, J. C. (1969): Dependence of desert rodents on winter annuals and precipitation. Ecology **50**, 721–724

Birkenstock, P. J.; Nel, J. A. J. (1977): Laboratory and field observations on *Zelotomys woosnami* (Rodentia: Muridae). Zool. Africana **12**, 429–443.

Bock, W. J.; von Wahlert, G. (1965): Adaptation and the form-function complex. Evolution, **19**, 269–299.

Brownfield, M. S.; Wunder, B. A. (1976): Relative medullary area: A new structural index for estimating urinary concentrating capacity of mammals. Comp. Biochem. Physiol. **55**, 69–75.

Christian, D. P. (1979 a): Comparative demography of three Namib Desert rodents: responses to the provision of supplementary water. J. Mammalogy **60**, 679–690.

Christian, D. P. (1979 b): Physiological correlates of demographic patterns in three sympatric Namib Desert rodents. Physiol. Zool. **52**, 329–339.

Christian, D. P. (1980): Patterns of recovery from low numbers in Namib Desert rodents. Acta Theriol. **25**, 431–450.

Emerson, S. B.; Bramble, D. M. (1993): Scaling, allometry, and skull design. In: The Skull. Vol. 3. Ed. by J. Hanken and B. K. Hall. Chicago, Illinois: Univ. Chicago Press. Pp. 384–421.

Frazetta, T. H. (1975): Complex adaptations in evolving populations. Sunderland, Mass.: Sinauer Associates.

Freeman, P. W.(1979): Spezialized insectivory: beetle-eating and moth-eating molossid bats. J. Mammalogy **60**, 467–479.

French, N. R.; Maza, B. G.; Hill, H. O.; Aschwanden, A. P.; Kaaz, H. W. (1974): A population study of irradiated desert rodents. Ecol. Monogr. **44**, 45–72.

Futuyma, D. J.; Moreno, G. (1988): The evolution of ecological specialization. Ann. Rev. Ecol. Syst. **19**, 207–233.

Gould, S. J. (1977): Ontogeny and phylogeny. Cambridge, Mass.: Belknap Press.

Grant, P. R. (1981): The feeding of Darwin's Finches on *Tribulus cistoides* (L.) seeds. Animal Beh. **29**, 785–793.

Hamilton, S.; Johnston, R. F. (1978): Evolution in the house sparrow – VI. Variability and niche width. Auk **95**, 313–323.

Herrera, C. M. (1978): Individual dietary differences associated with morphological variation in Robins *Erithacus rubecula*. Ibis **120**, 542–545.

Herring, S. W.; Herring, S. E. (1974): The superficial masseter and gape in mammals. Am. Nat. **108**, 561–576.

Hespenheide, H. A. (1973): Ecological inferences from morphological data. Ann. Rev. Ecol. Syst. **4**, 213–229.

Lay, D. M. (1972): The anatomy, physiology, functional morphology and evolution of specialized hearing organs of gerbilline rodents. J. Morph. **138**, 41–120.

Lewontin, R. C. (1966): On the measurement of relative variability. Syst. Zool. **15**, 141–142.

Moriarity, D. J. (1977): On the use of variance of logarithms Syst. Zool. **26**, 92–93.

Nel, J. A. J.; Sutterheim, C. J. (1973): Notes on early post-natal development of the Namaqua gerbil *Desmodillus auricularis*. Koedoe **16**, 117–125.

Nelson, T. W.; Shump, K. A. (1978): Cranial variation and size allometry in *Agouti paca* from Ecuador. J. Mammalogy **59**, 387–394.

Nie, N.H.; Hull, C. H.; Jenkins, J. G.; Steinbrenner, K.; Bent, D. H. (1975): Statistical package for the social sciences. 2nd ed. McGraw Hill, New York.

Olson, E. C.; Miller, R. A. (1958): Morphological Integration. Chicago, Illinois: Univ. Chicago Press.

Patterson, B. D. (1981): Morphological shifts of some isolated populations of *Eutamias* (Rodentia: Sciuridae) in different congeneric assemblages. Evolution **35**, 53–66.

Patterson, B. D. (1983): Grasshopper mandibles and the niche variation hypothesis. Evolution **37**, 375–388.

Perrin, M. R. (1986): Some perspectives on the reproductive tactics of southern African rodents. Cimbebasia **8**, 63–77.

Pulliam, H. R.; Enders, F. (1971): The feeding ecology of five sympatric finch species. Ecology **52**, 557–566.

Reichman, O. J.; Van de Graaff, K. M. (1975) Association between ingestion of green vegetation and desert rodent reproduction. J. Mammalogy **56**, 503–506.

Rothstein, S. I. (1973): The niche-variation hypothesis – is it valid? Am. Nat. **107**, 598–620.

Russel, A. P.; Thomason, J. T. (1993): Mechanical analysis of the mammalian head skeleton. In: The Skull. Vol. 3, Ed. by. J. Hanken and B. K. Hall. Chicago, Illinois: Univ. Chicago Press. Pp. 345–383.

Schmitt, L. H.; Kitchener, D. J.; How, R. A. (1995): A genetic perspective of mammalian variation and evolution in the Indonesian Archipleago: biogeographic correlates in the fruit bat Genus *Cynopterus*. Evolution, **49**, 399–412.

Smith, K. K. (1993): The form of the feeding apparatus in terrestrial vertebrates: studies of adaptation and constraint. The Skull, Vol. 3, Ed. by J. Hanken and B. K. Hall, Chicago, Illinois: Univ. Chicago Press. Pp. 150–196.

Soule, M.; Stewart, B. R. (1970): The "niche variation" hypothesis: a test and alternatives. Am. Nat. **104**, 85–97.

Thorington, R. W., Jr.; Heaney, L. R. (1981): Body proportions and gliding adaptations of flying squirrels (Petauristinae). J. Mammalogy **62**, 101–114.

Van Valen, L. (1965 a): Morphological variation and width of ecological niche. Am. Nat. **99**, 377–390.

Van Valen, L. (1965 b): The study of morphological integration. Evolution **19**, 347–349.

Van Valen, L.; Grant, P. R. (1970): Variation and niche width reexamined. Am. Nat. **104**, 589–590.

Weins, J. A; Rotenberry, J. T. (1980): Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecol. Monogr. **50**, 287–308.

WERNER, E. E.; GILLIAM, J. F. (1984): The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. **15**, 393–425.
WILLSON, M. F. (1969): Avian niche size and morphological variation. Am. Nat. **103**, 531–542.
WILLSON, M. F. (1971): Seed selection in some North American finches. Condor **73**, 415–429.
WILLSON, M. F.; KARR, J. R.; ROTH, R. R. (1975): Ecological aspects of avian bill-size variation. Wilson Bull. **87**, 32–44.

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